

RESEARCH PAPER

Invasive species over-stabilise the vegetation of a mobile dunefield, Manawatū, New Zealand, disrupting natural succession

Gillian L. Rapson¹, Ashley L. Murphy^{1,2}, Angelina R. Smith¹¹ Ecology Group, School of Natural Sciences, Massey University, Palmerston North, New Zealand² Fauna Science Team, Terrestrial Biodiversity, Department of Conservation, Christchurch, New Zealand

Corresponding author: Gillian L. Rapson (G.Rapson@massey.ac.nz)

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Abstract

Aims: Mobile, coastal dunefields around the world are under threat from invasive plants, which may out-compete native plant species. These aliens may also accelerate stabilisation of the dunes, to the complete exclusion of early successional native flora. In a mobile dunefield we examine the impact of the increasing abundance of alien species on substrate stability and successional trends of the native vegetation. **Study area:** Tawhirihoe Scientific Reserve, Manawatū, New Zealand. **Methods:** We recorded species' covers and environmental factors in quadrats placed randomly over the mobile dunefield, and analysed the vegetation and its successional patterns via multivariate analysis. We explored the degrees of stabilisation and nativeness, referencing changes over the last three decades. **Results:** Our analysis reveals seven vegetation types, three with a high native component and following an established successional trend, and the others becoming dominated by alien grasses and herbs, and associated with increasing dune stability. Biodiversity is trending towards aliens, especially behind the foredunes, and aliens occupy nearly double the area of the mobile dunefield as do natives. Coverage of unvegetated or mobile sand has declined to 21 % and is projected to decline further. **Conclusions:** Only the foredunes and dune-slack wetlands are now in a mostly natural state, while native rear dune vegetation is becoming rare, and natural succession appears to be interrupted. Alien species over-stabilise the dunefield, facilitating further alien invasion, the longer-term implications of which are unknown. Intervention to destabilise the dunefield seems the most viable management option.

Taxonomic reference: Nga Tipu o Aotearoa (<http://nzflora.landcareresearch.co.nz>) [accessed 10 Jan 2023].

Keywords

alien, community, dynamic, ephemeral, exotic, grass, invader, stabilise, weed, wetland

Introduction

Dunes worldwide are a major habitat for rare and specialist floras, hosting over 5,000 plant species, many of them local endemics (van der Maarel 1993). However, over the last century the global extent of coastal dunes has been greatly reduced from the original 446,500 lineal km (Luijendijk et al. 2018), impacting their specialist floras. In

highly human-populated areas such as the Mediterranean, only 20% of dunes are in natural condition, while most others have incurred at least some damage or even been destroyed (Cooper and Jackson 2021). Loss has also occurred in areas as diverse as Israel (Kutiel 2001), Wales (Rhind et al. 2013), Taiwan (Huang and Yim 2014), Argentina (Carretero et al. 2014), and South Africa (Lucrezi et al. 2014). The situation is the same for New

Zealand's dunelands (Hilton 2006), despite the relatively recent history of human settlement (< 800 years for the tangata whenua, Māori), and < 180 years for peoples of European descent (Wilmshurst et al. 2011).

There are three main categories of threat facing dunelands. First is their extensive use by humans as access points, settlement areas, and transfer centres for commercial, agricultural and silvicultural products (Martínez et al. 2008; Huang and Yim 2014; Lucrezi et al. 2014; Tordoni et al. 2019, 2021). While accommodation can be made for natural dune areas, even within conurbations (e.g., Huang and Yim 2014; Orchard and Schiel 2021), in some cases coasts are not seen as hosting biodiversity values at all (Goula and Sturm 2019). More amenable to successful conservation management are the issues of dune mobility, and the threat posed by alien or exotic invaders (particularly of dune-adapted species), and their role in accelerating stabilisation of dunes.

Dune stabilisation

Around the world about equal proportions of sandy coasts can be categorised as stationary, prograding or retrograding (Luijendijk et al. 2018). Within these categories, coastal dunes vary in their behaviours. Dunes may be fixed, in which case their vegetation is generally of later seral species at dense covers, with little to no bare sand visible (e.g., Kenfig dunes in Wales; Pye and Blott 2017), or open, with higher sand cover and early seral species (e.g., Cole Creek, New Zealand; Sykes and Wilson 1991), or actually mobile, as especially occurs on prograding coasts (e.g., Manawatū, New Zealand; Esler 1969; Abhar et al. 2015; Villacís Lozada and Rapson 2021).

Dune mobility can be aggressive, e.g., Holland (1983) recorded rates of inland movement of dunes exceeding 1 km per year. It can also be transgressive, where sand leaves the dunefield to impact on other land covers and/or activities (Esler 1970; Hesp 2001). This may result in managerial intervention to deliberately stabilise sand (e.g., Avis 1989; McKelvey 1999), often with little regard to the conservation values of native vegetation (Williams and West 2000; Gross et al. 2013; Gao et al. 2020; Brandt et al. 2021). Stabilisation has been such that Gao et al. (2020) reported 93% of mobile dunelands reviewed globally had experienced a loss of bare sand over the last 1.5 centuries. In New Zealand 70% of active dunes has been lost, reducing their area to about 40,000 ha (Hilton 2006).

Dunes can be stabilised by a variety of geo-technical methods, including emplacing structures, e.g., groynes, seawalls, break-walls and sand-fences (Nordstrom and Jackson 2013), or by geo-engineering, such as shaping foredunes and beach replenishment (Nordstrom 2014), or even by chemically forming stabilising soil matrices (e.g., Ghadr et al. 2022). A further technique, bioengineering, involves the planting of vegetation, often alien (Jenks and Brake 2001; Sigren et al. 2014). Introduced from Europe in the 1870s, the most widespread dune alien in New Zealand

is the dune-builder, *Ammophila arenaria* or marram. Extensively planted from 1910–1930's (McKelvey 1999), it had occupied 74% of dunelands by 1992 (Partridge 1992). Also deliberately used to stabilise dunes are a range of coniferous species, especially *Pinus radiata* (Californian Monterey Pine), which was trialled along the Manawatū coast, south-western North Island, New Zealand, from 1915 (Gadgil and Ede 1998). Widely planted from 1950–1980, it effectively eliminated dune transgressions for the lifetime of the trees. Growth was originally hampered by nitrogen deficiency (McKelvey 1999), so *Lupinus arboreus* (tree lupin) was introduced from California to ameliorate the deficiency (Gadgil 2002).

Stabilisers as invaders

New Zealand is rated a global hotspot for invaders (Heywood 1989; Dawson et al. 2017; Tordoni et al. 2021). New Zealand's vulnerability is a consequence of its recent settlement by both Māori and Europeans, coincident with development of agriculture, increased trans-oceanic traffic and previously lax border controls (Heywood 1989; Asmus and Rapson 2014). Dawson et al. (2017) reported that coasts are especially prone to invasion, and, not surprisingly, many alien dune stabilisers subsequently show themselves as invasive, spreading to other dune areas, and sometimes beyond. Habitat changes wrought by such invaders may also facilitate the invasion of other available aliens. In New Zealand, alien marram traps sand readily, burying the less competitive native sand-binders (Sykes and Wilson 1990; Hilton et al. 2005), and rapidly invading other native vegetation (Esler 1970; Hilton 2006). And of course silviculture, e.g., of pines, completely eliminates native dune vegetation and is an ongoing source of invaders (Peltzer 2018), while tree lupin has become invasive in dunes and waste areas, somewhat slowed by the spread of a fungal blight during the 1980's (Dick 1994; Gadgil 2002), to which it is now becoming adapted (GLR, pers. obs.). These aliens have the capacity to further stabilise mobile sand, increasing the threat level to mobile dunefields.

Aim

New Zealand is an exemplar of coastal invasion processes which, while completed in some parts of the world, are still under way in others. Approximately 10% of New Zealand's coastline is faced with dunes (Gadgil and Ede 1998). While some dunelands are well documented (Sykes and Wilson 1987, 1991; Roxburgh et al. 1994; Pegman and Rapson 2005; Murphy et al. 2012; Hilton and Konlechner 2022), most are poorly studied. Thus, their vulnerability to over-stabilisation and their exposure to alien invasions is equally poorly understood.

Our focal dunefield is Tawhirihoe (pronounced “Tar-firry-ho-e”) Scientific Reserve, the most important and most mobile dune reserve on the Manawatū coast of the

lower North Island. Various methods of sand stabilisation by bioengineering have been explored there for more than a century (Gadgil and Ede 1998). Other studies have focussed on botany (Carnahan 1957), dune dynamics (Esler 1970), particularly blowouts (Hesp 2001, 2002), and the nature and dynamics of dune slack wetlands (Esler 1969; Singers 1997; Yuhnevich 2015; Murphy et al. 2019; Villacís Lozada and Rapson 2021, 2022). Our aim is to assess the impact of alien invaders on dune mobility and on the succession of native vegetation, thus helping shape managerial responses.

Study area

Since the 1950's, the Manawatū district on the south-western side of the North Island, has lost the largest proportion (81.3%) of dunelands of any region in New Zealand (Hilton et al. 2000; Hilton 2006). By length of coastline only 7.2% of the dunelands is protected, in three reserves. Within the Foxton Ecological District, Ravine (1992) considered the most valuable remaining dune system to be Tawhirihoe Scientific Reserve (40°185'S, 175°135'E), which is just south of the village of Tangimoana on the southern bank of the Rangitikei River mouth, and 45 km north-west of the city of Palmerston North. The reserve was gazetted in January 2001, with ownership passing to the governmental Department of Conservation (Department of Conservation 2007). Tawhirihoe is roughly triangular, 152 ha in size, with 1 300 m of coastline, extending 800 m inland at its furthest point, and having a mobile dunefield of ≈ 48.7 ha (Figure 1). Fronted by coastal foredunes (Figure 2), though with some gaps or breaks, especially around the Rangitikei River mouth, deflation basins or slacks occur behind the foredunes. These are interspersed by remnants of the trailing arms (horns) of parabolic dunes (Carnahan 1957; Esler 1969, 1970), parabolaes being driven inland by the prevailing wind in a predominantly south-easterly direction (Esler 1969; 113° true north, Villacís Lozada and Rapson 2021). Stabilised dunes are found to the rear of the reserve, mostly now in pine plantations, within which a scrubland patch, known as the Fernbird area, hosts a range of largely native shrubs (Figure 1).

In 1913 trial plantings of marram (*Ammophila arenaria*) were conducted along the coastal edge of the Manawatū dunefield in attempts to prevent mobile dune transgression into farmland (Gadgil and Ede 1998; McKelvey 1999). This successfully slowed and even stopped foredune collapse (AKA mobility) for some decades (Gadgil and Ede 1998). Then in the 1980's most of the Tawhirihoe duneland was planted with alien *Cupressus macrocarpa* and *Pinus radiata*, as part of the wider Santoft dune stabilisation programme carried out by the New Zealand Forest Service (Singers 1997). Fortunately, in the main mobile dunefield (of Tawhirihoe), many seedlings were pulled out by conservation activists shortly after planting, and most of the remaining seedlings died. Further planting of marram at

the rear of the mobile dunefield also occurred at this time (Singers 1997), but, after conservational representations, land managers sprayed out tufts within the year (Colin Ogle, pers. comm. 2021). In the 2000's extensive reparatory plantings of foredune natives, especially *Spinifex sericeus* (Poaceae), took place to heal areas where the marram foredune had become too tall and had collapsed.

Dune slack wetlands are habitat for a range of specialist and threatened plant species, including *Eleocharis neozelandica* (Cyperaceae), *Isolepis basilaris* (Cyperaceae) and *Goodenia heenanii* (AKA *Selliera rotundifolia*; Goodeniaceae; Rapson 2018a; Murphy et al. 2019). These early successional species of short, open turf are adapted to a nutrient-poor environment with large seasonal water table fluctuations. Concern at the loss of this habitat in Tawhirihoe Reserve led to creation of new wetlands via the excavation of two artificial hollows in 1996 (Singers 1997, 1998), and a subsequent, much larger one in 2008. Succession of these hollows was studied by Murphy et al. (2019).

Several other nationally threatened species are found in the reserve, including the cryptic dune shrub *Pimelea arenaria* (Dawson et al. 2005). The nationally critical dune sub-shrub *Pimelea actea* (Rapson 2018a) was reintroduced into Tawhirihoe in late 1995 (Singers 1997) and spread to wetland margins. One of New Zealand's most endangered plants, only two small populations were known, here and at Castlecliff, near Whanganui (Burrows 2008), 43 km to the north-east. But the species apparently died out at Tawhirihoe about 2018, and the Castlecliff site was lost to land slips, so *Pimelea actea* is presumed extinct in the wild at this time (GLR, pers. obs.).

Methods

Sampling

In mid-summer of 2009/2010, vegetation was sampled using 52 quadrats, 1 m \times 1 m square, placed at random over the dry portions of the mobile dunefield of Tawhirihoe Scientific Reserve. Proportionately appropriate to the mobile duneland, an additional 12 wetland quadrats from those reported in Murphy et al. (2019) were randomly selected to represent the six wetlands.

Within each quadrat, the slope, maximum standing vegetation height, and percentage covers of sand (< 2 mm diameter), stones (≥ 2 mm diameter), wood and dead material, and live vegetation were recorded. Cover of each individual plant species was estimated as the vertical projection of all its foliage onto a horizontal surface, effectively recording its shadow under solar zenith (Rapson 2017). Aspect was also recorded for each quadrat and reported as the cosine of the angle in radians, so values closer to 1 are more northerly (i.e., warmer), while those closer to -1 are southerly. Visual estimation of soil moisture was on a 1 (dry) to 3 (wet) scale. Values of 1 (none) to 5 (extreme) were assigned reflecting the degree of disturbance from wind, rabbits and/or vehicles.

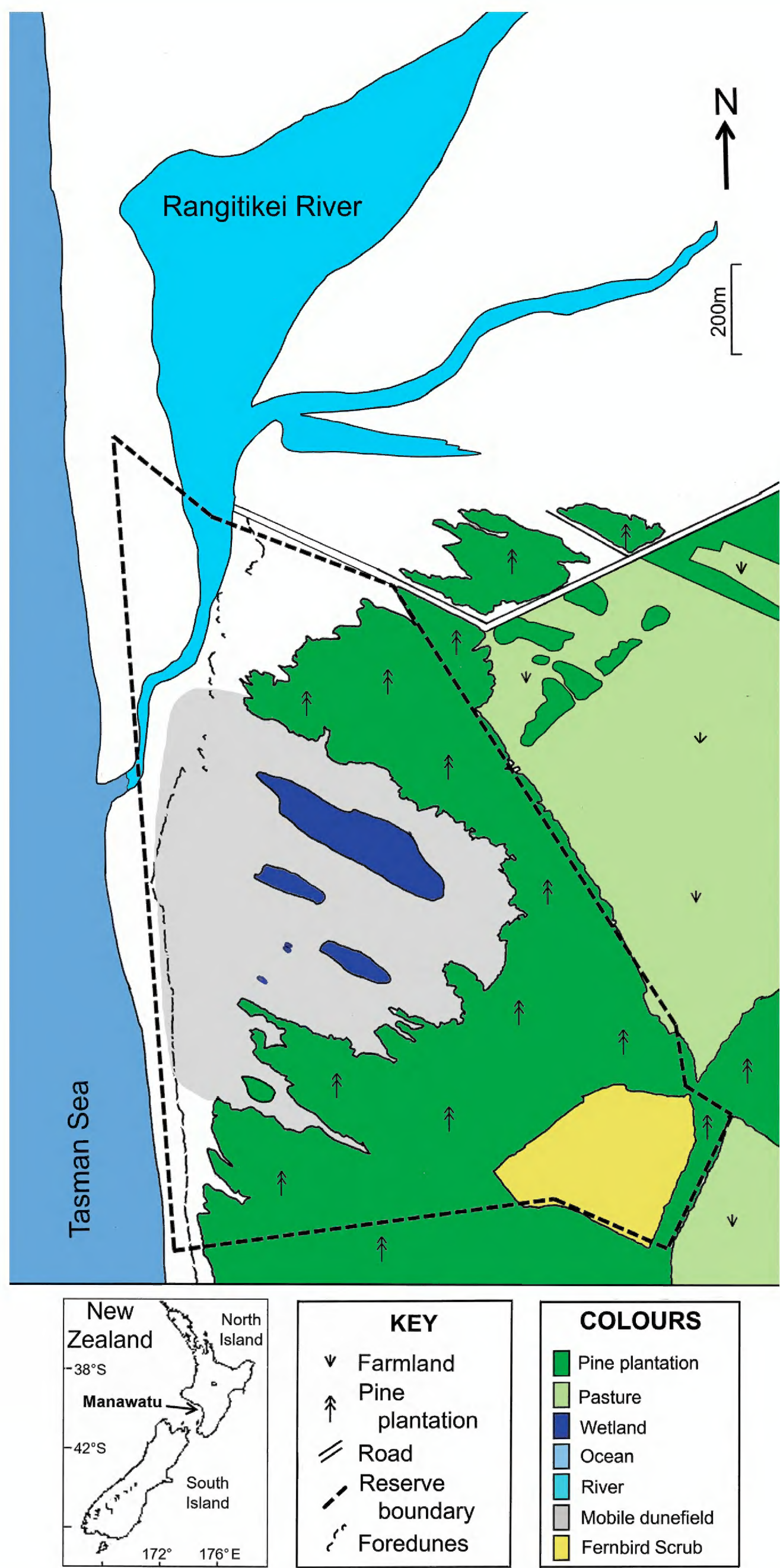


Figure 1. Location maps of the study site in New Zealand, and of the focal area of the mobile dunefield, and the surrounding pine plantation. The white area in the main diagram is a mix of bare sand, mud and estuarine vegetation associated with braiding of the Rangitikei River.



Figure 2. Aerial overview of the mobile dunefield in Tawhirihoe Scientific Reserve, looking nor-nor-east along the Manawatū Coast, with the Rangitikei River upper left, the village of Tangimoana upper centre, and farmland upper right. Within the reserve, the mobile dunefield is in fawn colours, surrounded by the dark green of *Pinus radiata* plantations. The image is prior to some major incursions of mobile sand. Image: Don Ravine, 1994, with permission.

Analysis

Data on percent covers (square-rooted) of species in each quadrat were clustered using Euclidean distance and Ward linkage metrics in SYSTAT (Systat 1998), to give a strong, though somewhat arbitrary, dendrogram. This was pruned to give seven vegetation types, accepted here as communities. A principal component analysis (PCA) of the untransformed data (to improve the spread of quadrats) was run in Canoco (ter Braak and Smilauer 2002). The community types from the cluster analysis were superimposed on the PCA's first two axes. For each community type, species' composition and environmental variables from each quadrat were averaged and tabulated. Community types were mapped from the sampling points (quadrats) overlain on the aerial photograph of 2012 (the only available date close to the field survey), and their area extrapolated using the pixel counter in Adobe Photoshop Co., San Jose, USA.

The importance of invasion by alien plants in the reserve was explored by calculating the relative cover ratio of natives and aliens, by species and by community type, and through fitting a contour plot to the spatial data for alien species' cover as a proportion of total cover, using linear interpolation following Lodwick and Whittle (1970) in Systat (1998).

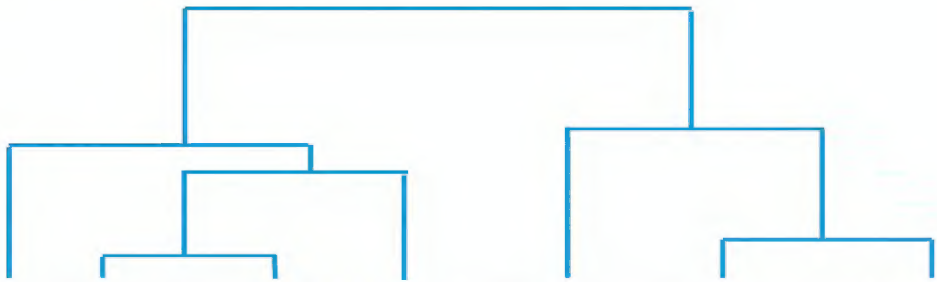
Changes in vegetative cover over time were inferred from the thesis of Singers (1997), extrapolating from his shoot-presence data and associated environmental measurements in 271 random quadrats of 2 m × 2 m over the mobile dunefield, as well as from personal knowledge (of GLR).

Results

Classification of vegetation types

Of the 64 random quadrats, three contained only bare sand and were on flattish sites, highly disturbed by wind and vehicles (Table 1). The remaining 61 quadrats had a mean vegetation cover of 60%. A total of 65 plant species was recorded, with 26 being native. On average, each species was found in 6.5 quadrats, with 22 species found in only one quadrat each. The most frequent species was the alien herb *Hypochaeris radicata* (found in 52% of quadrats), followed by four alien grasses, *Holcus lanatus* (46%), *Arrhenatherum elatius* (38%), *Lagurus ovatus* (36%) and *Ammophila arenaria* (33%). The most common native species were the sedge *Ficinia nodosa* (38%; wiwi) and the sand-binder *Spinifex sericeus* (25%).

Table 1. Mean environmental variables and summary features of the vegetation for each community, and for the quadrats containing only bare sand. For aspect, values closer to +1 are more northerly (i.e., warmer), while -1 is south. Soil moisture is scaled between 1 (dry) and 3 (wet), while disturbance is between 0 (low) and 5 (extreme).



Variate	Bare sand	Spinifex Foredune	Turfed Wetland	Sedge-land	Stone Plain	Oioi Rushland	Marram Duneland	Exotic Grassland
No. of quadrats sampled	3	9	3	15	11	5	13	5
Environment								
Distance to coast along slack (m)	291	193	361	539	359	447	357	434
Aspect (Northings)	0.800	0.101	1.000	-0.023	0.333	1.000	0.349	0.228
Angle of greatest slope (°)	3.7	8.8	0.0	6.5	6.7	0.0	9.3	10.4
Soil moisture	1.3	1.0	2.3	1.3	1.2	1.7	1.0	1.3
Wind disturbance	3.7	3.3	2.7	1.6	2.9	3.0	2.3	1.8
Vehicle disturbance	2.3	0.1	0.0	0.2	0.4	0.0	0.3	0.4
Rabbit disturbance	0.0	0.4	0.0	1.2	0.5	0.2	0.3	0.6
Sand cover (%)	100.0	73.1	35.0	9.4	84.7	8.4	47.7	1.0
Stone cover (%)	0.0	0.0	11.7	0.0	5.7	0.0	0.3	0.0
Wood cover (%)	0.2	0.1	0.0	1.8	0.4	0.0	0.5	3.0
Rabbit pellet cover (%)	0.0	0.1	0.0	0.1	0.1	0.0	0.0	0.0
Vegetation								
Vegetation height (cm)	0	48	55	100	66	128	84	131
Cover of live vegetation (%)	0.0	30.0	55.0	84.7	6.5	90.0	55.5	95.0
Cover of dead vegetation (%)	0.2	3.2	2.2	11.4	5.3	5.8	4.8	10.2
Total no. spp. in community	0	22	17	35	28	15	30	13
No. of alien spp. in community	0	16	3	29	19	7	23	10
Max. no. of spp. per quadrat	0	10	11	13	12	8	14	7
Mean no. of spp. per quadrat	0.0	5.8	8.7	8.8	4.1	6.0	9.9	5.8
Mean no. of alien spp. per quadrat	0.0	3.8	2.0	7.5	3.1	2.6	8.1	4.8
Mean cover of natives per quadrat (%)	0.0	26.9	32.7	15.3	1.3	71.0	16.1	5.7
Mean cover of aliens per quadrat (%)	0.0	5.3	24.7	76.3	5.6	20.5	43.3	94.7
Prop. per quadrat of vegetative cover as aliens	0.0	0.17	0.43	0.83	0.81	0.22	0.73	0.94

The dendrogram (Table 1) splits quadrats initially into two clusters, the first mostly with low sand cover and high abundance of aliens *Ammophila arenaria* and *Holcus lanatus*. The second cluster generally has much higher sand cover and abundance of two natives *Apodasmia similis* (oioi, pronounced oi’oi; Restionaceae) and *Ficinia nodosa*. These clusters were further divided into 3–4 communities each. The first two PCA axes (Principal Components Analysis; Figure 3) explained 22.0 and 12.6% of the variation in the data respectively. The second axis was influenced by native species, while the first responded to the high levels of alien grasses, though the composition of the latter was more variable.

Communities identified

Spinifex Foredune

Apart from a few small patches behind the parabolic dunes, to where the spiky, tumble-weed-like inflorescences of *Spinifex sericeus* are wind-dispersed, the Spinifex Foredune community forms the coastal edge of the Reserve, with a mean quadrat cover of 24% for Spinifex, which forms 80% of the vegetative cover (Tables 1, 2). It is the most exposed community, with a subjective wind disturbance score of 3.2/5 and with 73% sand cover (Table 1). Other

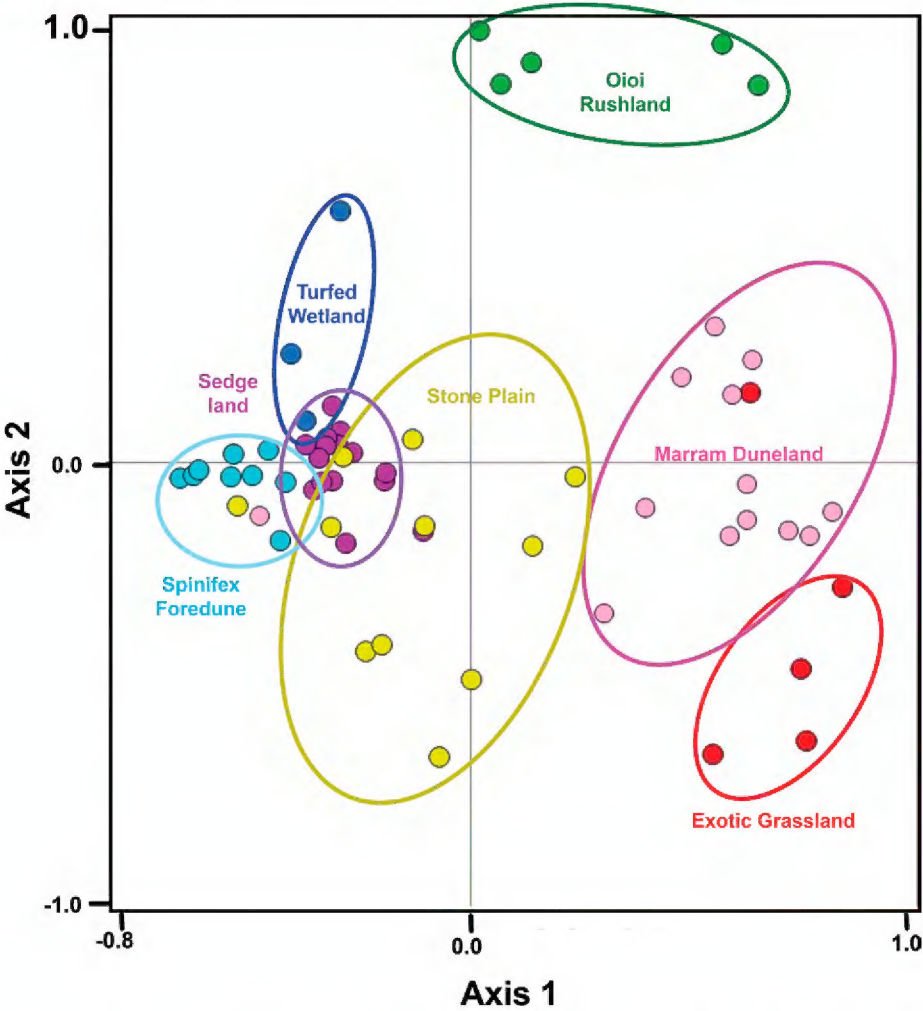


Figure 3. Principal Components Analysis of the sites sampled, with colours and ellipses (inclusive of most samples) identifying the seven communities recognised by the dendrogram.



native dune plants are occasionally present, including the slower-growing sand-binder *Ficinia spiralis* (pingao), the creeper *Calystegia soldanella* and the divaricating (i.e., with small leaves and tangled branches; Greenwood and Atkinson 1977) shrub of dunes, *Coprosma acerosa* (Rubiaceae; Table 2), making this the community most dominated by natives to 83% of the vegetative cover (Table 1; Figure 4A). The flatweed *Hypochaeris radicata* is the most important alien species, but at < 2% cover. Some marram is present, subject to occasional herbicidal control.

The next two communities, and Oioi Rushland and Exotic Grassland, are given names consonant with their composition as detailed in the wetland surveys of Murphy et al. (2019) in this same reserve.

Turfed Wetland

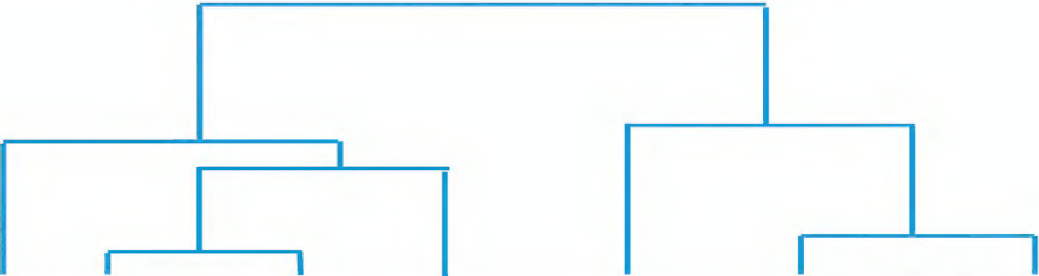
Turfed Wetland is an early successional stage of dune-slack wetlands, as reported by Murphy et al. (2019), and has the

wettest soil found in our survey (Table 1). This small community (Figures 4D, 5) is dominated (used in the sense of cover) by the milfoil, *Myriophyllum votschii* at 16% cover, with the local turf endemic, *Goodenia heenanii* common in patches, both < 2 cm tall. Some emergent *Apodasmia similis* and the small-dune builder, *Carex pumila* (Burgess 1984), are also present (Table 2, Figure 4D). *Schoenoplectus pungens*, a native freshwater cyperad to 40 cm, has occupied one end of the largest of the created wetlands (see Murphy et al. 2019 for details). The few alien species present attain 25% cover of each quadrat, with *Juncus articulatus* being aggressive at the eastern end of the southern-most wetland.

Sedgeland

The native sedge *Ficinia nodosa*, a component of both wetlands and low dunes, is common in Sedgeland, the most frequently sampled community. With low cover of bare sand, this community has 6 times as many alien

Table 2. Interesting species in the seven communities, and their average % covers, with the dendrogram above, and number of quadrats sampled from each community. Important values are shaded. (Covers of all species are listed in Suppl. material 1.) For status, a = alien, n = native. For habit, g = grass, h = herb, r = rush, sedge or similar, s = shrub.



Species	Status	Habit	Spinifex Foredune	Turfed Wetland	Sedgeland	Stone Plain	Oioi Rushland	Marram Duneland	Exotic Grassland
No. of quadrats sampled			5	5	15	9	13	11	3
<i>Ammophila arenaria</i>	a	g	0.6	0.0	0.9	1.1	0.0	14.4	17.0
<i>Arrhenatherum elatius</i>	a	g	0.0	0.0	9.3	0.4	3.0	2.0	51.0
<i>Dactylis glomerata</i>	a	g	0.0	0.0	2.7	0.0	0.0	0.9	0.0
<i>Holcus lanatus</i>	a	g	0.2	0.0	24.2	0.1	7.4	1.5	17.6
<i>Hypochaeris radicata</i>	a	h	1.2	0.7	3.0	0.2	2.1	1.6	2.1
<i>Juncus articulatus</i>	a	r	0.0	17.3	0.0	0.0	0.0	0.0	0.0
<i>Lagurus ovatus</i>	a	g	0.4	0.0	1.3	0.3	0.0	5.5	0.1
<i>Lotus pedunculatus</i>	a	h	0.1	0.0	13.5	0.0	5.0	0.4	4.0
<i>Lupinus arboreus</i>	a	s	0.1	0.0	5.8	1.1	0.0	1.5	0.0
<i>Medicago lupulina</i>	a	h	0.1	0.0	8.8	0.1	0.0	2.2	0.0
<i>Senecio glastifolius</i>	a	h	0.3	0.0	1.0	0.1	0.0	2.3	0.0
<i>Apodasmia similis</i>	n	r	0.0	5.2	0.9	0.0	55.0	0.0	0.6
<i>Calystegia soldanella</i>	n	h	1.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Carex pumila</i>	n	r	0.0	0.5	0.0	0.4	0.0	0.0	0.0
<i>Coprosma acerosa</i>	n	s	0.6	0.0	2.8	0.1	0.0	3.6	0.0
<i>Cordyline australis</i>	n	s	0.0	0.0	0.0	0.0	0.0	0.2	0.0
<i>Eleocharis neozelandica</i>	n	r	0.0	1.7	0.0	0.0	0.0	0.0	0.0
<i>Epilobium billardierianum</i>	n	h	0.0	0.2	0.0	0.0	0.2	0.0	0.0
<i>Ficinia nodosa</i>	n	r	0.0	0.0	10.6	0.1	12.0	5.2	5.0
<i>Ficinia spiralis</i>	n	r	0.6	0.0	0.0	0.4	0.0	0.0	0.0
<i>Goodenia heenanii</i>	n	h	0.0	3.0	0.0	0.0	0.0	0.0	0.0
<i>Isolepis cernua</i>	n	r	0.0	0.8	0.0	0.0	0.0	0.0	0.0
<i>Lachnagrostis billardierei</i>	n	g	0.3	0.2	0.2	0.0	0.0	4.5	0.0
<i>Lobelia anceps</i>	n	h	0.0	1.7	0.0	0.0	0.4	0.0	0.0
<i>Muehlenbeckia complexa</i>	n	s	0.0	0.0	0.0	0.0	0.0	1.4	0.1
<i>Myriophyllum votschii</i>	n	h	0.0	15.7	0.0	0.0	0.0	0.0	0.0
<i>Ozothamnus leptophylla</i>	n	s	0.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Pimelea actea</i>	n	s	0.0	0.0	0.0	0.0	0.2	0.0	0.0
<i>Schoenoplectus pungens</i>	n	r	0.0	1.0	0.0	0.0	0.0	0.0	0.0
<i>Schoenus nitens</i>	n	r	0.0	0.2	0.0	0.0	2.0	0.0	0.0
<i>Spinifex sericeus</i>	n	g	24.0	0.0	0.8	0.1	0.0	1.2	0.0
<i>Triglochin striata</i>	n	r	0.0	1.7	0.0	0.0	0.0	0.0	0.0

as native species, making up three quarters of its cover (Table 1). It is actually dominated by the aliens *Holcus lanatus*, *Lotus pedunculatus*, *Medicago lupulina* and *Lupinus arboreus*, a shrub widely planted on dunes, but self-introduced here (Table 2). Tightly structured in the PCA (Figure 3), the community is found throughout the middle of the Reserve on flatter, often south-facing areas.

Stone Plain

The remaining, predominantly native community is the Stone Plain, compositionally midway between the above communities and closely associated with them in the PCA (Figure 3). It has 6% stone cover amongst 85% sand, and mostly occurs in the south-western quarter of the reserve on flatter sites (Figure 5A). All four dune-builders (*Ammophila arenaria*, *Carex pumila*, *Ficinia spiralis*, *Spinifex sericeus*) are present here at very low cover (Table 2).

Oioi Rushland

Associated strongly with the larger, aggressive aliens in the species' dendrogram (data not presented) is the clon-

al restiad *Apodasmia similis*, which has numerous thin (≈ 2 mm), jointed stems standing to 100 cm tall, and appearing orange, brown or shadowy dark green on imagery (Figures 2, 4B). It dominates (to 55% cover) the Oioi Rushland community, which occurs on the floor of infilling wetlands (Figure 5A), showing only 8% bare sand. Interspersed with *Ficinia nodosa* to 12% cover, there is high coverage of natives (Table 1), including the creeping herbs *Epilobium billardarianum* and *Lobelia anceps*. It also contains the only sampled occurrence of the rare dune sub-shrub, *Pimelea actea* (Rapson 2018a), subsequently apparently extinct in the reserve and elsewhere (GLR, pers. obs.)

Marram Duneland

Marram Duneland is dominated by *Ammophila arenaria* at 14% cover, and *Lagurus ovatus* at 6% (Table 2), but the other alien grasses are less important, totalling < 10% cover, with almost 50% sand cover, and 3% wood cover, mostly of driftwood. *Coprosma acerosa* and *Lachnagrostis billardierei* (sand bent) are at their most abundant in this community (< 5%; Table 2, Figure 4C),

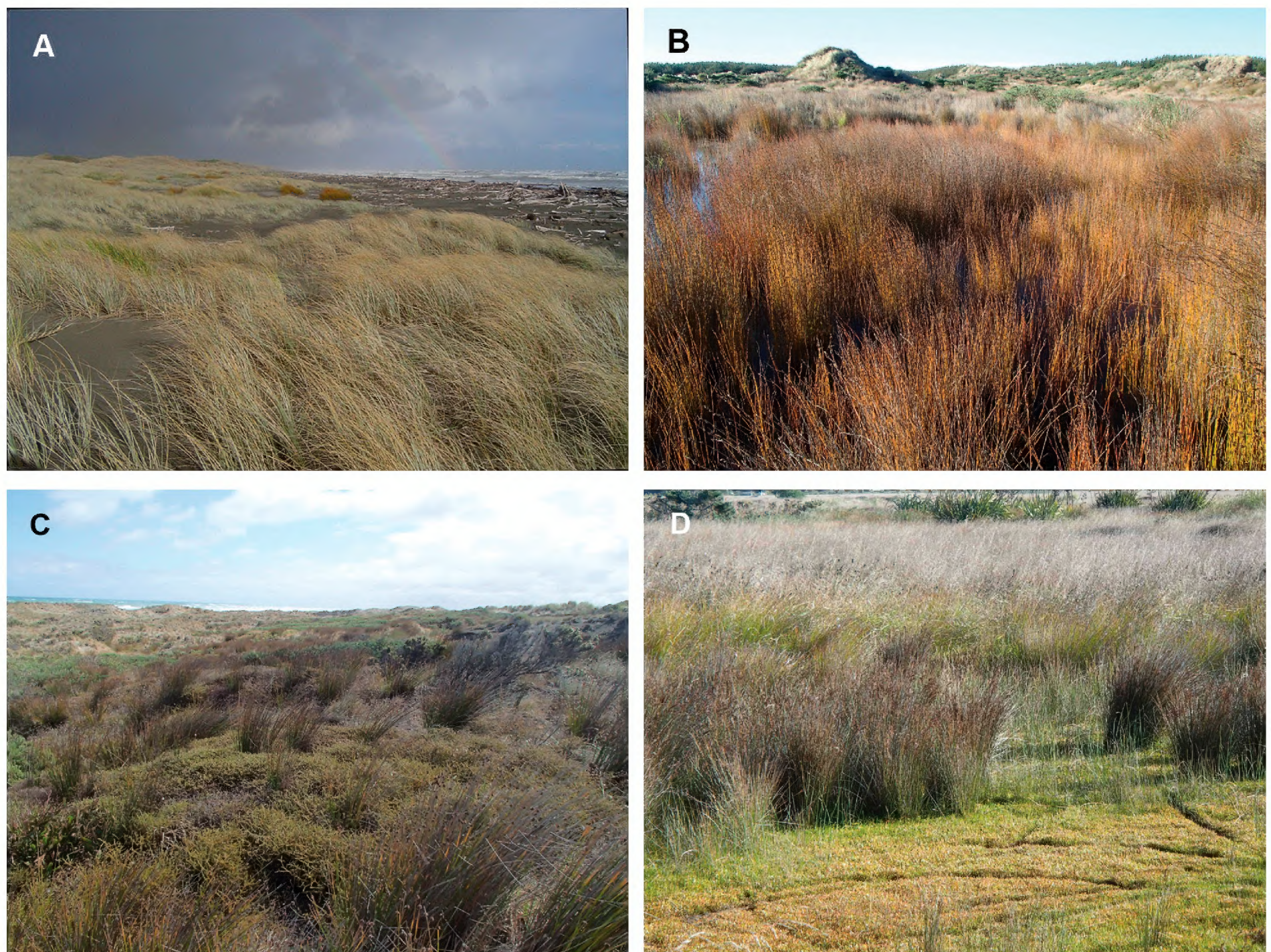


Figure 4. Tawhiriho Scientific Reserve. A) Spinifex Foredune Community, dominated by *Spinifex sericeus*, with a small, orange patch of *Ficinia spiralis* near centre top; Image: June 2008. B) Oioi Rushland, dominated by *Apodasmia similis* in standing water, with Marram Duneland in the background; May 2015. C) Prostrate shrubs of *Coprosma acerosa* amongst tufts of *Ficinia nodosa* from community Marram Duneland, on the rear of the foredunes; March 2022. D) Exotic Grassland in the mid-ground, dominated by flowering plants of the alien grass *Arrhenatherum elatius*, behind small clumps of restiad *Apodasmia similis*, and with a sward of *Goodenia heenanii* in Turfed Wetland in the foreground, disturbed by motor bikes; March 2019. Images: Jill Rapson.

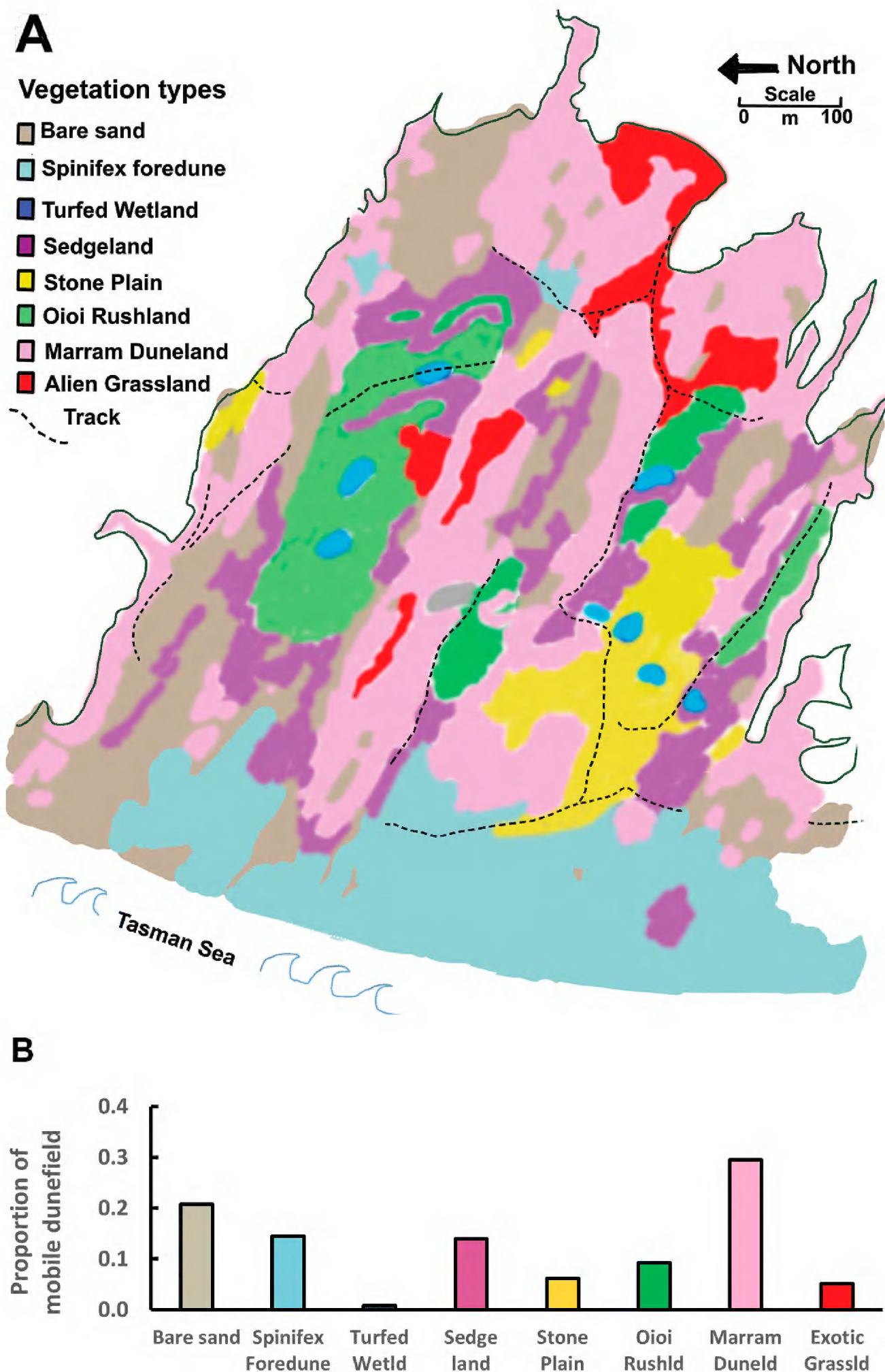


Figure 5. A) Detailed pattern of the vegetation of the mobile dunefield, interpolated from the samples overlain on an aerial photo dated 2012. Surrounding vegetation within the reserve is pine plantation. B) Proportionate cover of vegetation of the seven communities in the mobile dunefield.

along with occasional *Spinifex sericeus*, the scrambler *Muehlenbeckia complexa* (Polygonaceae), and small amounts of the mid-successional cabbage tree (*Cordyline australis*; currently in Asparagaceae). The community is the most widespread on the mobile dunefield (Figures 5A, 5B), occurring behind the foredunes and on steep slopes across the reserve.

Exotic Grassland

Exotic Grassland (name of Murphy et al. 2019), is dominated by the tall alien grasses *Arrhenatherum elatius* and *Ammophila arenaria*, as well as *Holcus lanatus*, to 85% cover, with very little bare sand (1%; Figure 4D). Some

alien herbs are also present, such as *Hypochaeris radicata* and *Lotus pedunculatus* (Table 2). The most abundant native is *Ficinia nodosa* at 5% cover. The community is scattered, though frequent on flatter ground at the rear of the mobile dunefield (Figure 5).

Invasion and stabilisation in the duneland

Changes since the first detailed survey of this area by Singers (1997) include the addition of 11 newly-recorded alien species, of which six are grasses, and the loss of 31

alien species, mainly wasteland weeds. One native species (*Tetragonia trigyna*, Aizoaceae, a species of shady sands) was added, though 14 were lost, including six species of early successional turf wetlands.

The spatial size of the largest wetland (numbered 1 in Singers 1997; Murphy et al. 2019), was greater in 1996 (Villacís Lozada and Rapson 2021, 2022). When analysed by Singers (1997), the wetland had an intermix of communities, covering the Turfed Wetland and Oioi Rushland types which we also identified. These are interspersed with “Exotic Grassland”, Singers’ version of which has high frequencies of *Holcus lanatus*, *Hypochaeris radicata*, *Leontodon taraxacoides* and the native *Ficinia nodosa* (Singers 1997). Thus, it somewhat resembles the Sedgeland community we report, though at lower vegetation cover. The other major change in the mobile dunefield is the loss of wetland turf vegetation in the south-eastern corner (Singers 1997), due to ongoing vehicular disturbance and infilling.

In our survey, the most widespread community is now Marram Duneland at 29% coverage of the dunefield, while the remaining communities contribute an average of 8% cover each (Figure 5B). In the five communities with > 55% cover of vegetation, alien species dominate in three (Figure 6A), which, broadly-speaking, occur in the rear portion of the reserve (Figure 6B). The cover-rich exceptions are Turfed Wetland and its later successional stage, Oioi Rushland, which are more centrally located, though even within these communities, about 20% of the vegetative cover is alien. Stone Plain is also dominated by aliens, but occupies only 6% of the mobile dunefield (Figure 5B). The greatest cover of natives (83%) is in Spinifex Foredune, which dominates the sea-wards edge of the dunefield (Figure 5A).

Overall, 21% of the studied area is still in mobile sand (Figure 5B), along with bare sand also exposed within communities. Averaging the communities by their contents and extrapolating proportionately across the dunefield, bare sand occupies another 33% of the visible surface. Increased cover of aliens appears associated with a decrease in the coverage of mobile sand (Figure 7A), for which changes over time show a loss rate of approximately 1% per annum (Figure 7B).

Discussion

Mobile coastal dunefields have their own unique flora and fauna, which are challenged by the extremely dynamic environment as well as arrival of invasive species. Seen as the enemy of successful dune management, movement of sand is usually anthropically restrained by technical or bioengineering means. The latter often introduces an alien plant species which can then go on to become invasive. That disturbance, and the modern availability of other aliens, can expose dune systems to ongoing invasion, further impacting on native biodiversity and successional processes.

In the holantarctic region, foredunes may be especially vulnerable to invaders (Tordoni et al. 2021). In the early stages of alien plant invasion, New Zealand’s dunefields

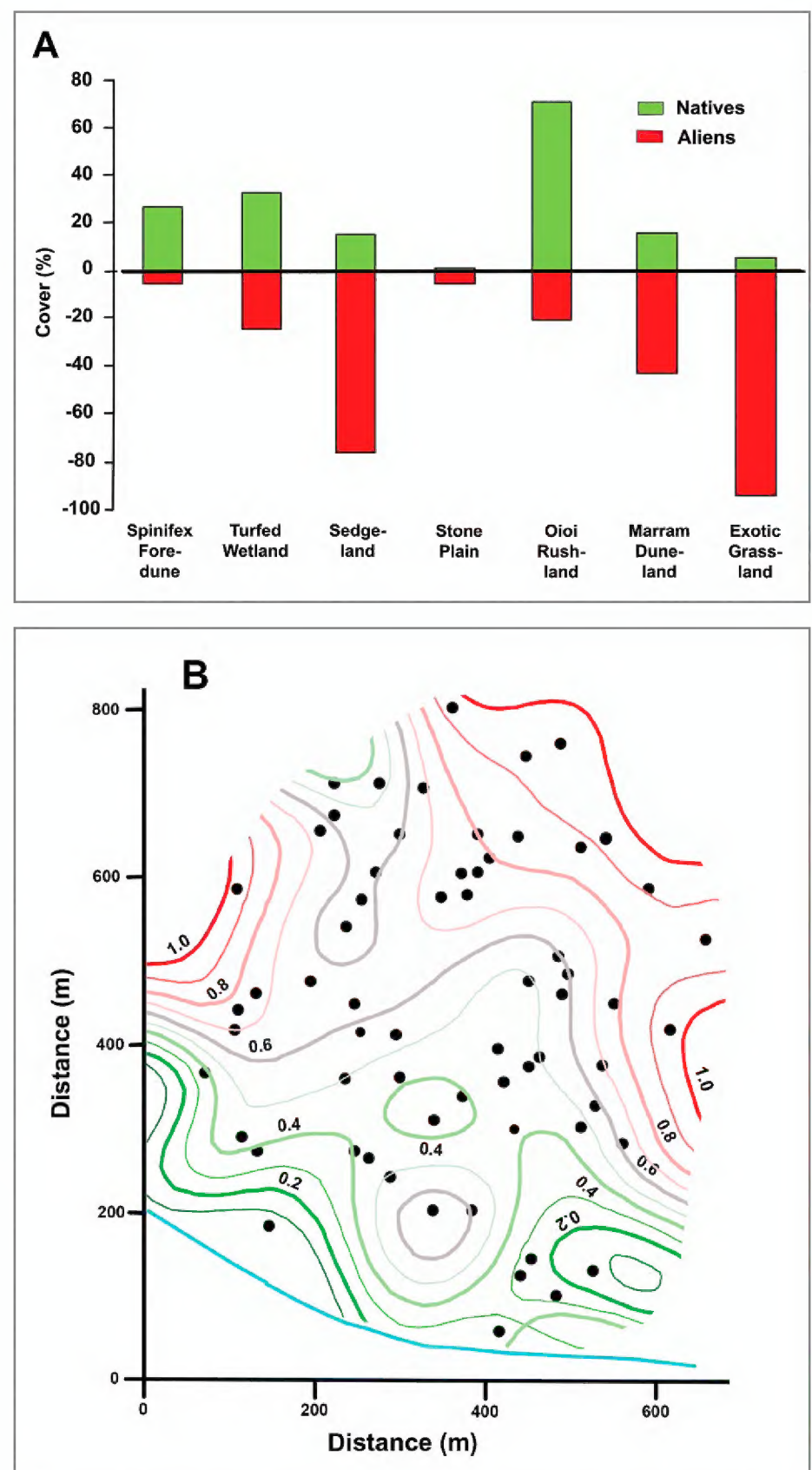


Figure 6. A) Cover of native (green, above the x axis) and alien (red, below) species in each community. B) Contour plot of the spatial distribution within the mobile dunefield of the proportion of the vegetation cover which is comprised of alien species. Red = more alien, green = more native, blue = plage.

offer opportunities to explore this invasion process, which is already well underway or perhaps completed in parts of the world with a longer history of human settlement.

Succession on the mobile dunefield

In New Zealand normal dune successions trend towards forested vegetation (Smith et al. 1985; Sykes and Wilson 1991; c.f. Pegman and Rapson 2005). But at Tawhirihoe Scientific Reserve only the second axis of our PCA depicts the natural succession, while the first axis is instead dominated by habitat types with a high cover and diversity of aliens (Figure 3), particularly alien grasses, such as marram.

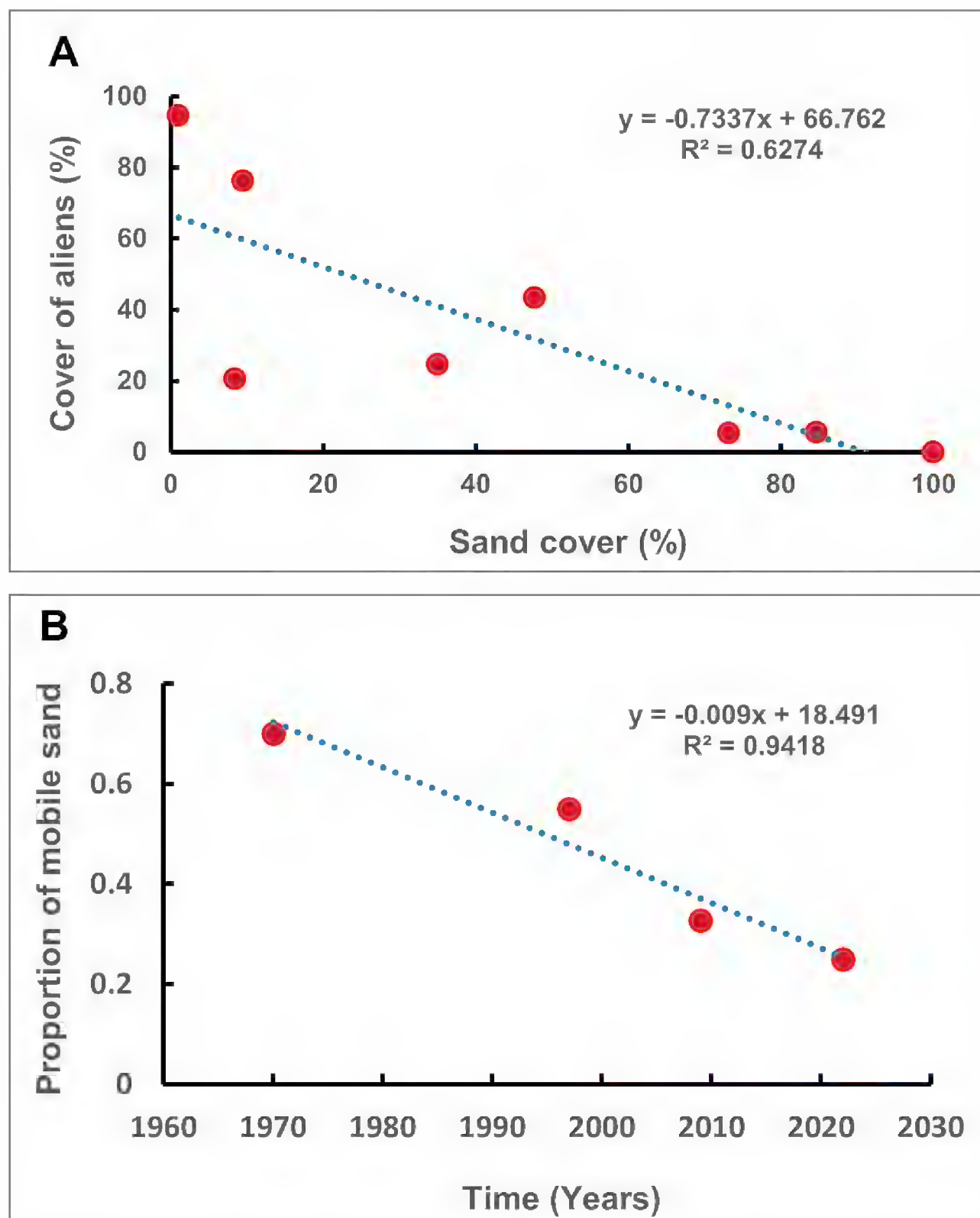


Figure 7. Relationships between A) covers of aliens and bare sand in each community, and B) proportional change of bare sand in the mobile dunefield over time. For B) the first and last values are based on literature and personal observations of GLR.

The native / marram balance on the foredunes

At Mason Bay, Stewart Island, in southern New Zealand, marram's invasiveness is demonstrated by its' covering 75 ha in 40 years (Hilton et al. 2005), and the need for a bi-decadal control programme to restore pristine-looking foredunes of pingao (*Ficinia spiralis*; Hilton and Konlechner 2022). Along the Manawatū coast there are occasional patches of pingao, some of which have been planted by iwi (local representatives of the indigenous people), who value the foliage for weaving. But pingao is not particularly common where sands are more mobile (Esler 1970), as *Spinifex* builds dunes faster. Marram builds foredunes even faster than *Spinifex*, though it is less salt-tolerant (Sykes and Wilson 1988). However, marram dunes eventually become over-steepened, and destabilise (Figure 8A).

The *Spinifex* Foredune is the most natural community at Tawhirihoe, and despite low levels of invasion by alien dune specialists (e.g., *Carpobrotus edulis*) and hardy generalists (e.g., *Hypochaeris radicata*), is probably simi-

lar to that occurring before European settlement (Cockayne 1909, p. 15; Johnson 1992; Partridge 1992; Pegman and Rapson 2005). *Spinifex*'s long, downward-flowing rhizomes root readily into fresh sand (Cockayne 1909), repairing erosion of, and undercutting of, the foredune, such as occurs during tidal or storm surges, so that it can out-compete marram on active foredunes (Esler 1970). Since the Manawatū coast is prograding (Hesp 2001; Villacís Lozada and Rapson 2022), management is now required to vegetate the foredunes with *Spinifex* (Figure 8B) to counteract the earlier plantings of marram (Cockayne 1909; p. 12; McKelvey 1999).

Succession on the rear dunes

Marram persists mainly on the rear dunes and parabolic horns of blown-out foredunes (Verhoeven et al. 2014). Pegman and Rapson (2005) also recorded an *Ammophila* Dune community at Whatipu Beach, near Auckland city, upper North Island, where the coast has prograded so rapidly that those dunes were short and well inland. Isolated from the maritime influence, that community is also



Figure 8. Vegetation change over time at Tawhirihoe Reserve. A) Marram turret being undercut by an inland movement of the Rangitikei River mouth; note four juvenile *Homo sapiens* for scale; March 2007. B) Restoration planting of *Spinifex* to form a new foredune where movement of the Rangitikei River mouth has exposed fresh sand in front of an earlier restoration planting of a marram foredune; August 2008. C) The site of Wetland 1 inundated in a wet winter, backed by Oioi Rushland, and surrounded by dunes vegetated with alien shrubs, including *Lupinus arboreus* in the foreground and *Acacia sophorae* in the background; October 2022. D) Looking across Wetland 2 towards Wetland 6 in an area formerly in Oioi Rushland, Marram Duneland and Stone Plain, showing aliens to $\approx 70\%$ cover; October 2022. Images: Jill Rapson.

almost completely dominated by alien species, but with pingao and *Carex pumila* as additional sand-binders. Its successional fate is unknown.

Predictably, at Tawhirihoe the Marram Duneland community dominates the parabolic horns and rear dunes. Open, at about 50% bare sand, half of the vegetation is in aliens, and half of that in marram, though *Lagurus ovatus* is common too. While small native grasses (e.g. *Lachnagrostis billardiarei*) and dune shrubs are present, they account for only about a quarter of the vegetative cover (Table 1). Marram Duneland's successional fate is probably of increased coverage of shrubs, hopefully native, though the fate of the Fernbird area (Figure 1) and the patterns shown on our ordination (Figure 3) suggest otherwise.

Exotic Grassland, with low and pasture-like diversity, is the outlier community on Axis 1 of the PCA (Figure 3), and occurs mostly at the rear of the mobile dunefield. It is eponymous with the marram-dominated community of Murphy et al. (2019), but with the recent addition of *Arrhenatherum*

elatius, unrecorded by Singers (1997) or Ogle and Singers (2001). Densely vegetated by aliens, with almost no bare sand, this community has no known correspondents in other dunelands, and its successional future is unknown, but probably involves invasion by scrub weeds or other aliens.

Wetlands - rare habitats under threat

The dune slack wetlands, already reported by Esler (1969), Murphy et al. (2019) and Villacís Lozada and Rapson (2021 2022), were not the focus of this study, but the Turfed Wetland community here aligns with that of Murphy et al. (2019), as a later successional stage to native communities containing several rare turf species < 5 cm tall. Of these, only *Eleocharis neozelandica*, *Myriophyllum votschii*, and the local endemic *Goodenia heenanii* were sampled here, along with the nationally widespread *Isolepis cernua*, mostly at low cover. Though *Eleocharis neozelandica*'s presence was the prime motivator for the gazetting of Tawhirihoe Reserve (Department of Conservation 2007), it and other

turf species have died out locally, despite several attempts at creation of suitable wetland habitat (Singers 1997, 1998; Murphy et al. 2019).

The Turfed Wetland community contains only three alien species, though at 43% of total cover, but this proportion increases as the habitat infills with aeolian sand and dries out (Murphy et al. 2019; Figure 8C). Thus, the continuance of any specialist wetland turf species is problematic, depending on the intersection of ongoing wetland emergence, either naturally or anthropogenically, on dispersal by the turf species, and ongoing invasion by aliens.

Succession in the dune slacks

Murphy et al. (2019) reported that Oioi Rushland was successional to Turfed Wetland. Oioi forms dense thickets of thin stems to 1+ m tall and is found throughout New Zealand in dune slacks and estuaries (Cockayne 1909; Deng et al. 2004; Jupp et al. 2007). In Oioi Rushland half the species are alien, including *Lotus pedunculatus* and *Holcus lanatus*, though only to 20% of the vegetation's cover. Though isolated in the ordination (Figure 3) by the dominance of aliens, there is no marram in this community, and at Tawhirihoe it still appears part of the normal successional sequence.

The same alien species present in Oioi Rushland are in Sedgeland, but totalling 76% of the vegetation's cover, and bare sand is rapidly disappearing (GLR, pers. obs.; Figure 8D). Normally Sedgeland appears to be a successional stage (Murphy et al. 2019) into drier vegetation containing shrubs > 2 m tall, e.g., *Coprosma propinqua*, *Leptospermum scoparium* (Myrtaceae) and *Olearia virgata* (Asteraceae), though none of these were sampled here. Climax vegetation of dune slacks is probably tall forest of kahikatea (*Dacrycarpus dacrydioides*; Podocarpaceae) and pukatea (*Laurelia novae-zelandiae*; Monimiaceae), such as now persists in the sole forested dune slack reserve, Omarapapaku (Carnahan 1957; Esler and Greenwood 1968), about 4 km from the coast, and 13 km south of Tawhirihoe. However, intermediate stages past shrubland are unknown, and whether such succession is possible in the presence of alien invaders is also unknown.

The Stone Plain, which Singers (1997) called Dune Plain, is an unusual coastal feature. The rounded cobbles (< 20 cm diameter), are unlikely to have been emplaced from offshore sources, and instead may mark a prior location of a mouth of the nearby Rangitikei River. No such river mouth has been known over the last 140 years (Shand and Shepherd 2016), but given the current coastal progradation rate (1 m yr⁻¹; Hesp 2001; Villacís Lozada and Rapson 2022), its deposition probably occurred ≈ 180 years ago during early European-settlement-accelerated deforestation and subsequent erosion. Stones were estimated by Singers (1997) as 30% cover, while we recorded only a third of this, probably due to decadal-scale infilling by aeolian sand. Vegetation in the Stone Plain is sparse, but predominantly alien and increasing in cover (GLR, pers. obs.; Figure 8D). The ultimate successional fate of this community is unknown, but ongoing shrub invasion (c.f. Sedgeland) is indicated.

Role of invaders in dunelands

In New Zealand problems with alien weeds are immense, especially on conservation lands (Williams and West 2000; Howell 2008). At Tawhirihoe ≈ 70% of the reserve is planted in alien pine to “protect” farmland in the hinterland from dune mobility. The remainder of the reserve, the mobile dunefield, has 31% coverage of aliens, from 39 species. Of the 31 alien species recorded by Singers (1997), all still occur in the Manawatū, and most are probably still present within the reserve, so that their absence from the mobile dunefield probably reflects small differences in habitat availability or sampling, or random turnover of invaders. With 11 new species recorded in this survey (unlikely to have been missed by Singers (1997)), these alien-dominated communities seem to be accelerating the invasion of other aliens.

A portion of these alien species inevitably becomes extremely aggressive, influencing the ecology of the mobile dunefield. The nearby Rangitikei River estuary was the invasion site of European horsetail, *Equisetum arvense*, introduced by a local herbalist about 40 years ago. Resistant to all control efforts there (Esler 1978; Horizons 2013), horsetail subsequently spread into Tawhirihoe Reserve. Randomly unsampled in this survey, it is present in Exotic Grassland, and currently forms aggressive swards in disturbed drainage ditches around the periphery of the reserve. Another major weed is *Senecio glastifolius*, a South African asterad of fynbos, locally called pink ragwort (CABI 2017). It forms thickets in the rear dunes, with semi-woody tufts to 2 m tall, and has a canopy of bright pink capitula in mid spring, with vast seed production and pappus-based dispersal (Beautrais 2013; CABI 2017). Very invasive, several years of management at Tawhirihoe have failed to keep it in check, due to constant reinvasions from coastal populations situated to the north-west across the Taranaki Bight. In 2006 two individuals of *Osmunda regalis* (royal fern) were found amongst Oioi Rushland in the centre of Wetland 1, around a falcon “nest” (a terrestrial scrape; *Falco novaeseelandiae*). First recorded from the nearby Rangitikei region (Field 1890), royal fern is considered a conservation threat to wetlands in New Zealand (Howell 2008), as it displaces smaller native species (Martin 2002). At Tawhirihoe the plants were removed and vouchered (MPN 42111), and no reoccurrence has been noted. Also present at Tawhirihoe, though not sampled, *Acacia sophorae* (sand or golden acacia; from Australia's east coast) is a very invasive shrub, forming dense thickets 3–6 m tall, offering no habitat for native species. Herbicided in the past, the remaining plants continue to pose a threat, but hope is held for biocontrol using a bud-galling wasp (EPA 2022). Tawhirihoe Reserve should be monitored for such weeds, and any infestations immediately managed.

Consequences of dune stabilisation

Two of Tawhirihoe's communities dominant on Axis 1 of the ordination are essentially alien (Figure 3). Such com-

munities can cause reduction of native biodiversity and abundance, and loss of rare native species due to over-stabilisation (Acosta et al. 2009; Verhoeven et al. 2014; Tordoni et al. 2021).

Is native biodiversity being lost?

Only $\approx 10\%$ of Tawhirihoe Reserve is actually in native vegetation, dominated by the *Spinifex* Foredune, which is closest to the sea and the earliest successional phase of the dunes. Here species are more exposed and specialised, exhibiting highly adaptive characters (Acosta et al. 2009; Murphy et al. 2012; Verhoeven et al. 2014), which make them competitive in opposition to most aliens currently present.

Unsampled in our survey was native sand daphne (*Pimelea arenaria*; Thymeleaceae), a shrub to 1 m, formerly common on moderately-steep lateral dunes (Cockayne 1909, p. 21; Dawson et al. 2005), though not frequently noted by Singers (1997). Out-competed by tree lupin and other alien shrubs, and already of conservation concern (Dawson et al. 2005), it appears to be about to succumb to the fate of its even rarer dune congener, *Pimelea actea*.

A consequence of invasions further inland appears to be the generation of scrub-weed communities. Singers (1997) recorded a community type differing from those we describe, which he called the “Shrub Dune” community. Small-leaved shrubs which are highly branched (e.g., *Ozothamnus leptophyllus*; Asteraceae) or even divaricating (e.g., *Coprosma acerosa*) were frequent, occurring on very steep sites between the foredunes and dune slacks. While occasional *Coprosma* was recorded in our survey, very little *Ozothamnus* was encountered, with the few present occurring on the currently broad tops and rears of the foredunes, where the species still appears to be competitive against aliens. Shrub Dune is possibly the natural successional precursor to short, dry-land trees such as *Kunzea robusta* (Myrtaceae) and *Dodonea viscosa* (Sapindaceae), stands of which occur on dry sand ridges or the trailing arms of parabolic dunes, in patches along the Manawatū coast and a few km inland. This forest could itself be successional to dry dune forest, probably of *Alectryon excelsus* (Sapindaceae) and *Podocarpus totara* (Esler 1978; Rapson 2018b), though this remains unclear (Esler 1978).

Are dunes being over-stabilised?

Estimates of the loss of mobile sand dunes in New Zealand over the last 70 years range from 60–80% (Ryan et al. 2023). The equivalent value for Tawhirihoe’s mobile dunefield is 62%, similar to that of the nearby Himatangi dunefield (6.5 km south; Ryan et al. 2023). Thus only 10% of Tawhirihoe Scientific Reserve’s surface area is currently in mobile sand, this proportion decreasing steadily over time (Figures 7B, 8). At the current rate of loss there will be no mobile dunefield inside the Reserve by 2045.

Much of this loss of mobility seems due to anthropic and invader-driven dune stabilisation. Alien species of dunelands are functionally dissimilar to natives and adopt less conservative strategies (Murphy et al. 2012; Verhoeven et al. 2014; Tordoni et al. 2019). Thus, their invasion

leads progressively to homogenisation, both floristically (e.g. for urban areas, Asmus and Rapson 2014), and functionally (Verhoeven et al. 2014; Tordoni et al. 2019), a consequence which appears worldwide (Ricotta et al. 2014). Where native vegetation is considered during dune stabilisation at all, biodiverse dunes are often preferred (Acosta et al. 2009), such as are usually found at later stages of succession (Pye and Blott 2017). In fact, stabilisation may “lock in” particular successional stages (Cooper and Jackson 2021), which may be managerially more desirable (Prach 2023) than allowing normal succession to progress.

Our results indicate that native early-successional species or species of foredunes may be especially prone to being lost as a result of alien invasions. In many parts of the world such impacts may have happened so long ago that they are unrecorded. New Zealand may be unusual, if not unique, in still undergoing such losses today, so that conservation management is still possible. However, such management may be hampered by lack of understanding of the degree to which mobility is a pre-human or natural situation for such dunelands (Esler 1978).

Potential management approaches

Though sometimes mis-directed (Cooper and Jackson 2020), deliberate disturbance to increase dune mobility can be considered a viable management technique (Bird et al. 2020). At Tawhirihoe, the presence of 1.6 km of off-road vehicle tracks in the mobile dunefield (in addition to numerous tracks throughout the pine forest) shows the extent of on-going human disturbance (Figure 5A). Many attempts have been made to protect the native vegetation, but informational signage is largely uninfluential, while excluding vehicles using fencing works only temporarily; even when wires do not get cut, fences are quickly buried by mobile sand. New vehicle routes are formed continually, though in areas of mobile sand, tracks also dissolve rapidly, except for now unreachable remnants which may persist as landscape features for decades. Contrarily, intermittent traffic helps to keep the dunelands open, as the associated compression and disturbance kills larger plants, especially aliens, and lowers the sand surface closer to the water table, providing habitat for rare turf species. For example, when the traffic route through the middle of the south-eastern-most wetland noted by Singers (1997) became inaccessible, the wetland dried out and lupin scrub invaded. But as a management tool, traffic is too unpredictable and illimitable to be effective.

Bird et al. (2020) recommended grazing as a tool to disturb dunes. But no mammalian grazers are indigenous to Tawhirihoe’s dunes. Instead, alien deer (red and sambar) are increasing in the duneland and surrounding plantations, due to reduced hunting during the Covid pandemic, but also in response to the increasing availability of alien herbage which dominates their sand-country diet ($> 90\%$ by weight; Stafford 1997). Since their introduction in the 1850’s (King 2017), rabbits have always been common on

New Zealand's dunes, and while persistent herbivores of aliens, they do more harm than good, probably having a role in the loss, perhaps extinction, of the subshrub *Pimelea actea* (Rapson 2018a).

Though counter-intuitive, destabilising the sand so that it moves inland (Hesp 2002), seems the most cost-effective option for retention of rarer natives. Breaching the foredunes, perhaps by herbiciding *Spinifex* would successfully remobilise some sand, and allow the natural formation of dune slacks and perhaps their associated wetlands. But the most likely result inland of the foredunes would be reinvasion of aliens, unless ongoing selective weeding occurs to favour natives.

Conclusions

Loss of mobile dunefield is a global trend, to which New Zealand dunelands are not immune despite the relatively recent history of human disturbance. At Tawhiriho, despite some small wetlands naturally reforming and deliberate wetland creation, habitat for rare turf species is being progressively lost. Planting of a *Spinifex* foredune and intermittent weed control especially of marram and woody species has been effective. But other management has been less so, due to the increasing influence of alien invaders.

The country-wide presence of marram-dominated dunes, and ongoing homogenisation of the alien flora, will continue to impact on New Zealand's mobile dune environments. It seems inevitable that the abundance and diversity of native dune flora will progressively decline, except perhaps in the most extreme sites such as frontal dunes or freshly-formed wetlands.

The global success of coastal aliens is likely to be exacerbated by changing climates, especially via changes

in storm patterns, even in areas with few human influences (Gao et al. 2020). There is currently little managerial will to effect anthropic coastal retreat, despite it being a desirable response to climate change (Haasnoot et al. 2021), and with an attendant opportunity to promote the restoration of coastal habitats to native vegetation. Further research and action is needed to mitigate this potential loss of native species and communities to alien invaders.

Data availability

The floristic data of the individual quadrats sampled in Tawhiriho are available in Suppl. material 1.

Author contributions

GLR and ALM designed the survey; ALM and ARS conducted the survey; ALM compiled the data and drafted the report; GLR compiled the paper.

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E-mail and ORCID

Gillian L. Rapson (Corresponding author, G.Rapson@massey.ac.nz), ORCID: <https://orcid.org/0000-0001-8108-9577>

Ashley L. Murphy (amurphy@doc.govt.nz), ORCID: <https://orcid.org/0000-0002-8463-1357>

Angelina R. Smith (smithmcbrydie.ar@gmail.com)

Supplementary material

Supplementary material 1

Table showing the individual and their vegetative contents, as % cover quadrats grouped according to community type.

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